Nipping the bud hypothesis: A comparison of savanna and forest tree responses to canopy scorch

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Abstract

Tree mortality, following surfaces fires, is much greater in forests than in savannas, despite similarities in the bark thickness of tree trunks. This difference is thought to influence the distributions of forest and savanna biomes. There is no consensus and very little research on how fires actually kill trees. Though tree canopies are too high above the flames to be charred, leaves are often scorched over the full tree height; hence the focus on differences in tree canopy recovery. I explored two possible mechanisms for differences in crown resprouting following canopy scorch: (1) differences in bud banks and their insulation, (2) differences in the vulnerability to disruption of the hydraulic system by heat scorch. I simulated canopy scorch using nine congeneric savanna-forest pairs in three Reserves in KwaZulu Natal, South Africa. Contrary to predictions, there was no difference in the presence of a viable bud bank between congeneric species. The resprouting response varied between congeneric pairs with only the *Combretum, Rhus* and *Acacia* pairs showing savanna species with a significantly greater ability to resprout. The vulnerability to hydraulic disruption was measured using wood density as a proxy for conduit reinforcement. The results are inconclusive and possibly affected by the growth rates of certain shade-tolerant forest trees. The differences in crown resprouting following canopy scorch of forest and savanna trees is not the result of differences in bud banks and resprouting ability. The differences in insulation of vulnerable tissue by bark may be related to the protection of the hydraulic system rather than the buds and/or cambium.

Introduction

There is considerable interest in the ecological community on the influence climate change will have on current biome distributions. The limitations to accurate modelling and predictions of change arise partly from the insufficient understanding of the factors and processes which define current biome boundaries (Hoffman *et al*, 2003; Midgley *et al*, 2010). This is evident in South Africa where forest and savanna biomes sporadically occur adjacent to one another with seemingly very abiotic few factors influencing this distribution. Longman and Jeník (1992) classify several ecological concepts for 'boundaries'; one such concept is the transition zone or ecotone between two biomes. This transition zone can be gradual with factors such as altitude, latitude or soil characteristics defining the change. Alternatively, the transition zone could be sharp and occur over a couple of metres. This sharp transition zone is common in the forest-savanna ecotones of South Africa. Another 'boundary concept' from Longman and Jeník (1992) is that of a barrier or a restraint on movement. In the context of this study, 'movement' is the occurrence of forest trees within savannas, and the proposed barrier or restraint to this 'movement' is the difference in fire-adaptive traits.

The evolutionary histories of savanna and forest species lead to different responses to naturally occurring fire. Savanna trees live in a very flammable grassy matrix and are burnt at intervals of 1 – 3 years in mesic and humid regions (Hoffman *et al*, 2009). The recruitment problem for juveniles is overcome by below ground storage and a pole-like architecture (Archibald and Bond, 2003). However studies of adult savanna fire survival traits have largely focused on bark thickness, especially in the flame zone (Hoffman *et al*, 2003; Gignoux *et al*, 1997). Though canopies usually are not burnt, leaves and branches are scorched from heat. The effect of scorching has been poorly understood. Forest trees seldom burn because of the lack of grasses and a humid understory. Fires in forests typically lead to much higher tree mortality than in savannas (Cochrane, 2003).

Comparative studies on forest and savanna tree traits are highly dependent on the age class of the individuals and the selective pressures associated with the age class (Archibald and Bond, 2003, Bond and Midgley, 2001). This study focuses on adult individuals from savanna and

forest species. Bond and Midgley (2001) emphasise the importance of persistence traits in community assembly whereby adult individuals show varying resilience to disturbance in rates of survival and the ability to recover through sprouting (Keith *et al*, 2007). Studies of persistence traits (e.g. Hoffman *et al*, 2003, 2009) have focused on traits such as bark thickness, total non-soluble carbohydrate storage in roots and stems and the height of reproductive individuals. Few comparative studies have explored the differences between post-fire canopy recovery of forest and savanna species, specifically on the differences in canopy recovery through sprouting.

In this study, I compared savanna and forest species focusing on traits commonly associated with fire resistance. I particularly wished to explore differences in post-fire canopy recovery between forest and savanna species. Though tree canopies are too high above the flames to be charred, leaves are often scorched over the full tree height. Savanna trees, which experience frequent fire, would require protected or insulated buds to recover rapidly from crown scorch (Burrows, 2002). Forest trees, where fires are unlikely catastrophic events, may have no such protection from crown scorch. Though, where studies have compared buds of eucalypts, which have fire resistant crowns, with other species; I know of no studies comparing forest and savanna crown sprouting traits.

Bark properties are often proposed as the main reason for tree survival in fire (Gignoux *et al*, 1997; Hoffman and Solbrig, 2003, Balfour and Midgley, 2006). Bark thickness is a particularly important property, the ability to insulate heat sensitive tissue (cambium, xylem, bud tissue, phloem) within the stem is stated by some as "the primary factor determining whether a tree is fire resistant or not" (Reifsnyder *et al*, 1967; Bond and van Wilgen, 1996), however Gignoux *et al* (1997) caution against such an over simplification. Forest trees primarily compete for light therefore it is expected that savanna trees will show greater investments in bark in than forest trees.

So the hypothesis is that savanna canopies recover faster from crown scorch than forest trees, which may not recover at all. This would result in high mortality from a surface fire in a forest, but none at all in a savanna (Browne, *Unpublished*). There are two possible mechanisms

for differences in forest and savanna crown sprouting (1) differences in bud banks and their insulation, (2) differences in the vulnerability to disruption of the hydraulic system by heat scorch (Midgley *et al*, *in press*). There is no consensus and very little research on how fires actually kill stems of savanna trees (Midgley *et al*, 2010). I explored both possible mechanisms here.

These hypotheses were tested in Northern Kwa-Zulu Natal, South Africa, using congeneric species pairs containing one forest species and one savanna species, preferably from the same genus. This was not always possible as was the case with marula, *Sclerocarya birrea,* and wild plum, *Harpephyllum caffrum*. In comparative studies, it is imperative that there is a measure of phylogenetic independence, which can be accounted for using congeneric pairs (Felsenstein, 1985; Hoffman *et al*, 2003).

Methods

Field work for the study was conducted in three Ezemvelo Kwa-Zulu Natal Wildlife (EKZNW) reserves in Northern Kwa-Zulu Natal, South Africa. The preliminary field work was done in March 2010 and was concluded in August 2010. Nine forest-savanna species pairs (Table 1) were chosen based on the availability of these species within the EKZNW reserves (Figure 1). The majority of these species were found within the Hluhluwe-iMfolozi Park, whilst Ithala Game Reserve and the Isimangaliso Wetland Park False Bay Nature Reserve contained one each.

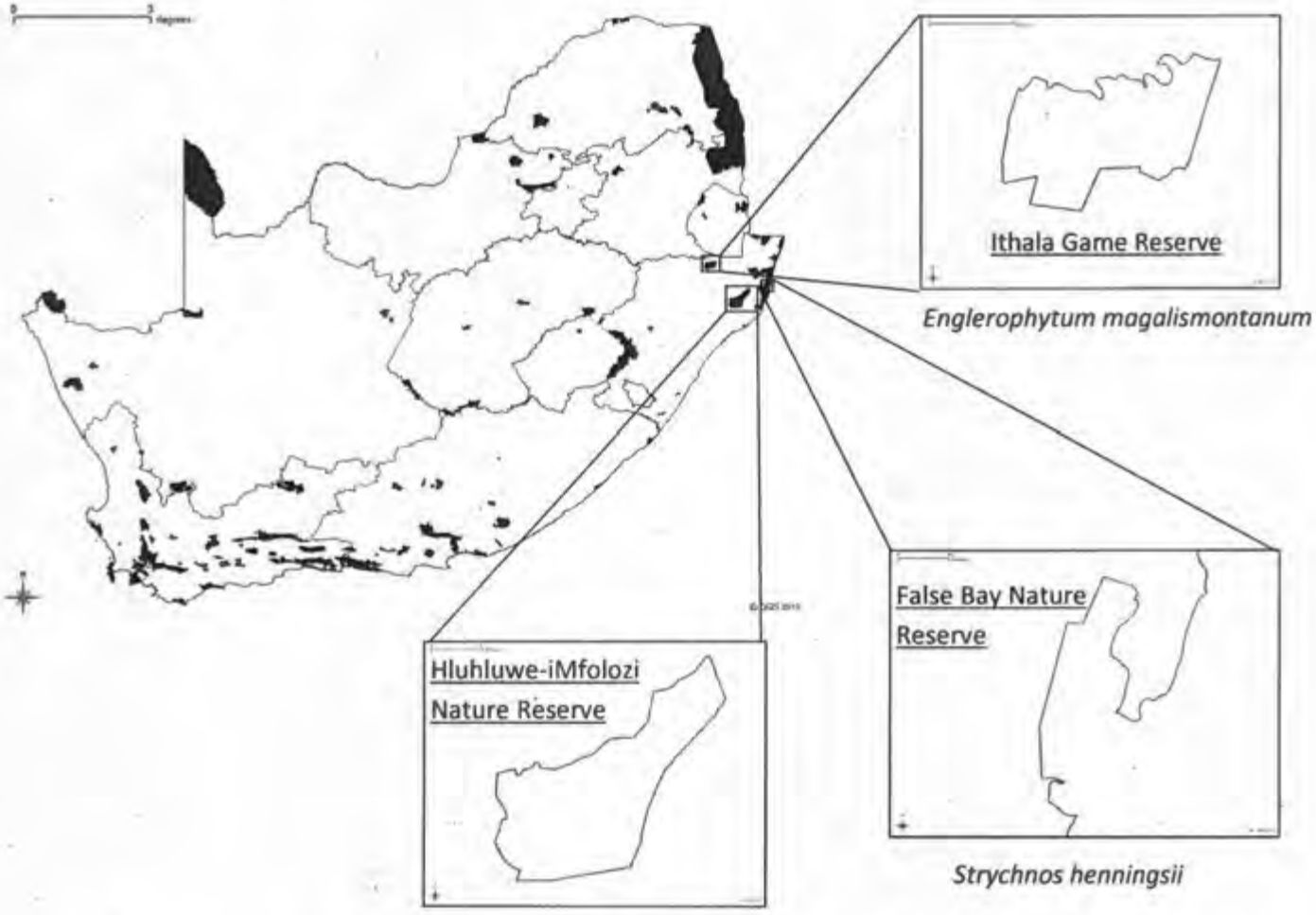

Figure 1. Location of the reserves in which the study was done. The species investigated in Ithala Game Reserve and False Bay Nature Reserve are shown below their respective inserts. The remaining species were found in the Hluhluwe-iMfolozi Park.

The three reserves contain elements of savanna and/or forest biomes. The Hluhluwe-iMfolozi Park (28°12'41"S 31°59'31"E) extends over 960 square kilometres and is roughly divided by the Corridor Road into the wetter Hluhluwe in the north and the drier iMfolozi in the south. This summer rainfall region receives between 600m and 1000mm *per annum*. The Ithala Game Reserve (27°31'41"S 31°17'55"E) occurs at a higher altitude, 400m a.s.l. – 1450m a.s.l. This 300 square kilometres summer rainfall region receives between 750mm and 1000mm *per annum* and occasionally experiences extreme winter frost. The predominantly upland mesic savanna (Archibald and Bond, 2003) is intersected with densely vegetated riverine valleys and high-lying grassland plateaus. The False Bay Nature Reserve (28°00'34"S 32°21'20"E) forms part of the Isimangaliso Wetland Park, a World Heritage Site. The reserve is found on the Western shores of False Bay, part of Lake St. Lucia. This is the smallest of the three reserves, covering 225 square kilometres. Vegetation in the park is primarily thornveld, lowland savanna and sand forests. Rainfall (600mm *per annum*) and altitude for False Bay Nature Reserve are less variable than the other parks.

Table 1. Congeneric species pairs studied.

Savanna Species	Forest Species	Family
Dombeya rotundifolia	*D. burgessii*	Sterculiaceae
Euclea divinorum	*E. racemosa*	Ebenaceae
Combretum molle	*C. kraussii*	Combretaceae
Sclerocarya birrea	*Harpephyllum caffrum*	Anacardiaceae
Rhus pentheri	*R. chirindensis*	Anacardiaceae
Acacia karroo	*A. robusta*	Fabaceae
Englerophytum magalismontanum	*E. natalense*	Sapotaceae
Maytenus senegalensis	*M. mossambicensis*	Celastraceae
Strychnos madagascariensis	*S. henningsii*	Loganiaceae

Congeneric Pairs

The treatments and measured variables were performed on congeneric species pairs, comprising a savanna and forest species of the same genus (Table 1). An exception to this was the Anacardiaceae pair where marula, *Sclerocarya birrea*, and wild plum, *Harpephyllum*

caffrum, were paired. Felsenstein (1985) recommends this approach for comparative studies to ensure some level of phylogenetic independence, an approach which has been adopted by similar studies (Hoffman *et al*, 2003; Hoffman *et al*, 2004; Hoffman *et al*, 2009).

Sampling methods

Ten individuals of each of the eighteen species were sampled. Large individuals were selected so as to exclude juveniles which could exhibit different strategies to adult individuals (Bond and Midgley, 2001). Similarly, when possible, older branches were selected for experimental treatment to avoid innate differences between recent resprouts and established branches. An estimate of tree height was taken at each tree as well as trunk diameter at 1m above the ground.

Treatment

In March 2010, canopy scorch was simulated using a cutting technique with the diameters at which the branches were cut as a surrogate for measures of fire intensity. Firstly, a 1cm stem diameter was located and cut. The branch was then tagged 1m along the stem from the cut. Any branches between the original cut and the tag were also cut so that the terminal stem diameter of any branch was 1cm (Figure 2). This process was then repeated on a separate branch for a 3cm stem diameter. The treatment was replicated on ten trees of each of the eighteen species giving a total of 180 trees.

Measurements

An estimate of tree height was taken at each tree as well as trunk diameter at 1m above the ground. Bark thickness was measured at both the 1cm and 3cm diameters. A measure of bark thickness was also taken from the trunk at 1m above the ground. Bark thickness measurements were made using vernier callipers. A measure of stem architecture was taken by measuring the stem diameter at 5cm, 20cm and 100cm from the shoot tip.

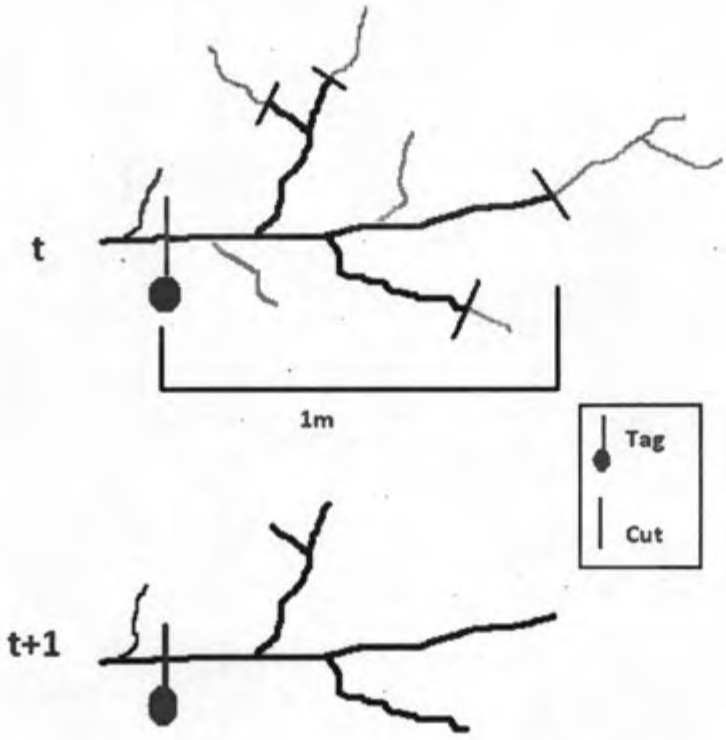

Figure 2. A schematic representation of the treatment

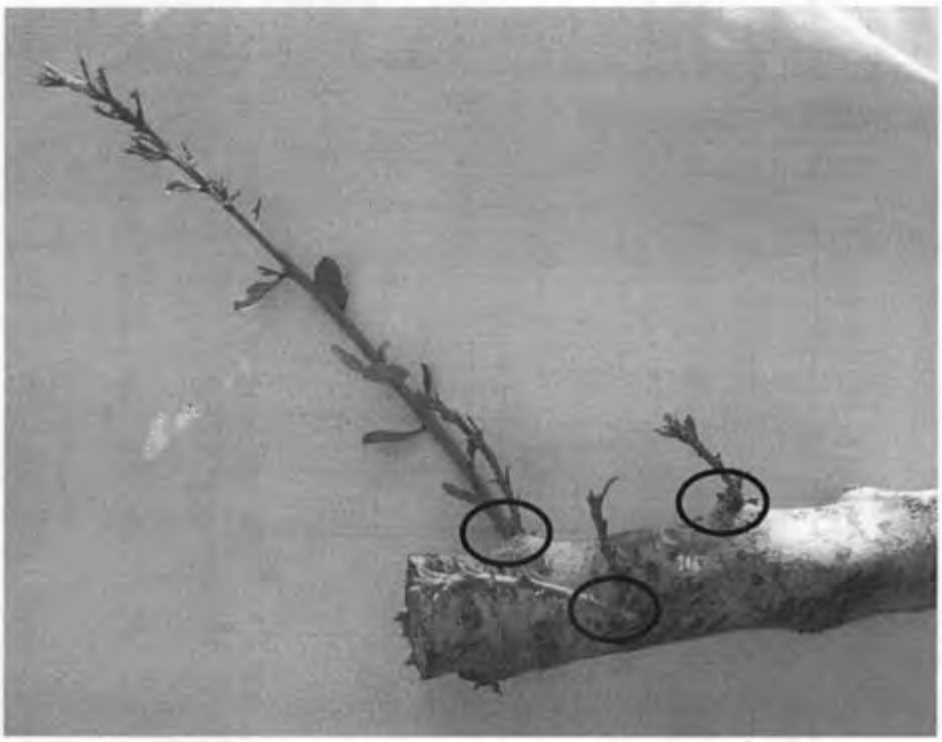

Figure 3. Photo of *Maytenus senegalensis* post-treatment sprouting in August 2010. The circles show the procedure used for counting the number of buds i.e. this branch has 5 resprouts from 3 buds.

I quantified resprouting of each individual in August 2010. I counted the number of resprouts found on the original 1m stretch of both the 1cm and 3cm diameter branches (Figure 3). This process was then repeated for the number of buds from which these resprouts grew (Figure 3). The length of each resprout was also recorded sequentially from cut to tag.

A section of stem (±3cm diameter) was collected from six individuals of each species excluding *Dombeya rotundifolia* and *D. burgessii* (controlled management burns in the Hluhluwe-iMfolozi Park in early August 2010 scorched the *D. rotundifolia* used in the study; so that the *Dombeya* pair, had to be excluded). The sections of stem were used to determine Stem Specific Density (SSD) using the protocol outlined by Cornelissen *et al* (2003). The bark was removed and the volume of the fresh stem was calculated using Archimedes Principle. Next, the wood samples were oven-dried at 100°C for six days and then weighed. The SSD was calculated as this mass divided by the volume.

Data Analysis

The data were analyzed using Statistica 9, R 2.11.1 and Microsoft Excel

A least-squares regression was used to fit a curve to the relationship between log-transformed bark thicknesses and stem diameters of all species and then of each congeneric pair. A least-squares regression was also used for the relationship between 3cm stem diameter bark thickness and wood density for the all species.A non-parametric Mann-Whitney U-test was used to compare differences in savanna and forest species pairs for absolute and relative bark thickness, stem architecture and resprouting capability.

The stem architecture measurements were used to determine the gradient at which stem diameter increases. The 1cm bark thickness value for each savanna species was then substituted into the corresponding forest species bark thickness regression to determine the diameter at which the same absolute bark thickness was reached (Figure 4). This diameter was then used in the stem architecture regression to determine the relative amount of canopy die back from the same intensity fire for savanna and forest trees (Figure 4).

A least-squares regression was used to fit a curve to the relationship between wood density and bark thickness for the mean values of all species. A Kruskal-Wallis multiple comparison test was used to test for significant differences between

A quantile regression was used to fit a curve of a 0.95 quantile to the relationship between tree height and the number of sprouts. This was done for both treatments of all the savanna and forest species.

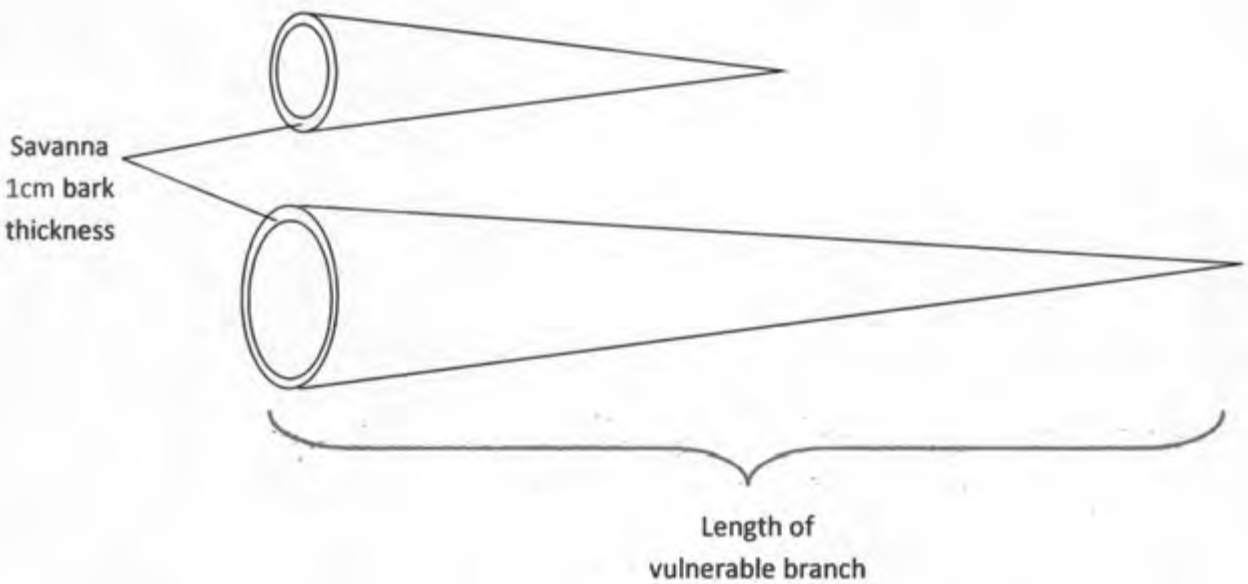

Figure 4. Schematic representation of the canopy die back analysis. The top and bottom branch represent a savanna and forest tree respectively.

Results

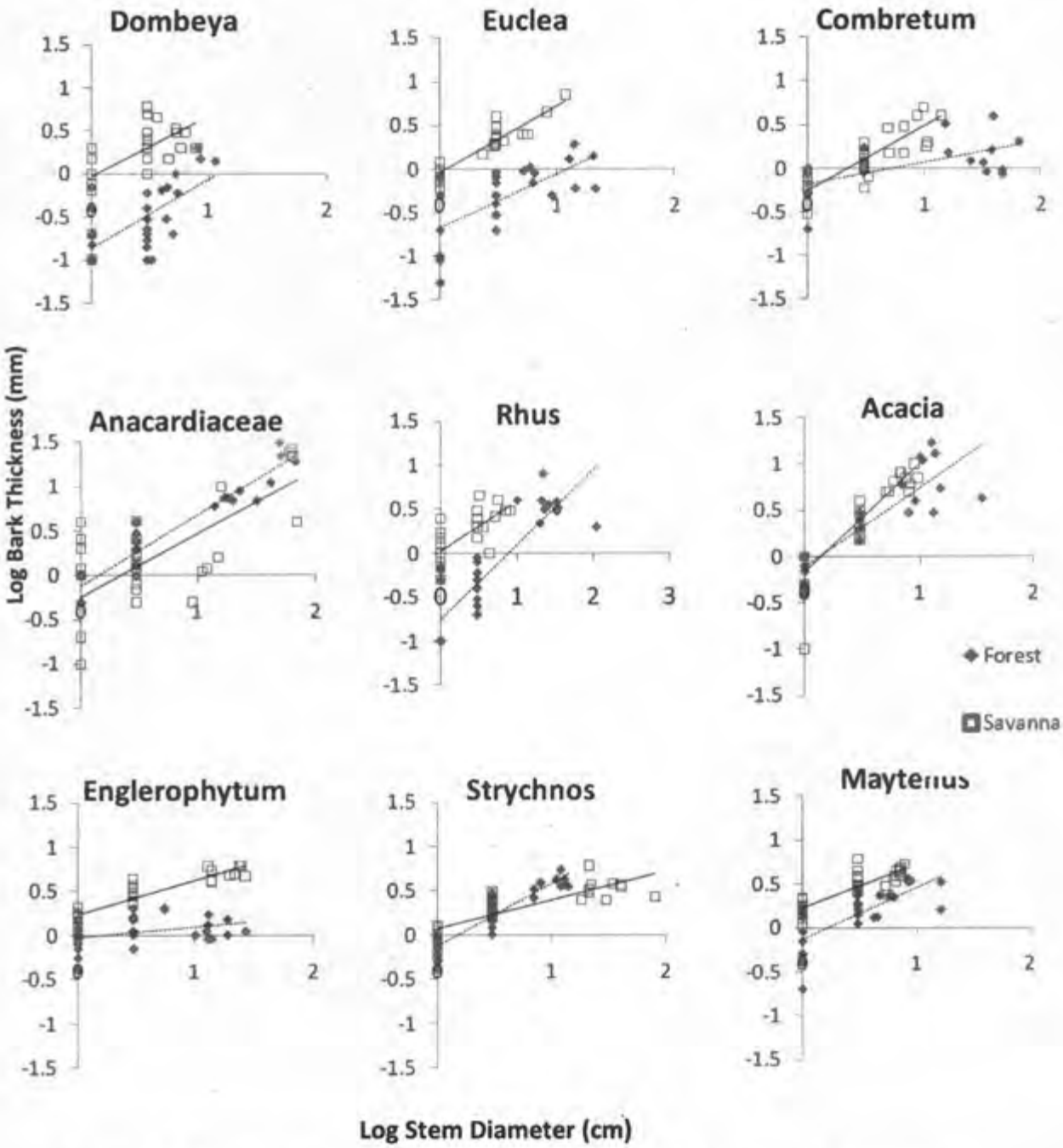

Figure 5. Relationship between stem diameter and bark thickness of congeneric savanna and forest trees. Both axes are log-transformed. See Table 1 for species names. Dotted line and solid line indicate Forest and Savanna regressions respectively. Statistics are listed in Appendix 1.

For four of the nine congeneric pairs the bark thickness for a given stem diameter was greater in the savanna species (Figure 5). In the Anacardiaceae pair, *Harpephyllum caffrum* showed greater bark thickness across the range of diameters ($y=0.7996x - 0.1207$, $R^2=0.8973$, $p<0.0001$, $n=30$), although this difference to its savanna pair was not statistically significant (Mann-Whitney U-test: See Appendix 2). Savanna absolute bark thickness at a stem diameter of 3cm and at the 1m trunk height was greater than the forest counterpart for seven (excluding *Anacardiaceae and Strychnos*) of the nine pairs (Appendix 2). *Combretum kraussii* and *Acacia robusta* showed higher bark thickness at 1cm stem diameters than their respective savanna counter parts (Figure 5).

Bark thickness for the combined savanna species and forest species (Figure 6) show savanna trees to have a higher overall bark thickness. The rate at which bark thickness increases is, surprisingly, slightly greater in forest species ($y = 0.6227x - 0.3365$, $R^2 = 0.39$, $p < 0.0001$, $n = 270$) than in savanna species ($y = 0.5798x + 0.0101$, $R^2 = 0.47$, $p < 0.0001$, $n = 270$). There are relatively low levels of correlation between bark thickness and stem diameter for savanna ($R^2 = 0.47$) and forest ($R^2 = 0.39$) trees; however within congeneric pairs, the savanna species generally show higher levels of correlation ($R^2 > 0.5$) while forest species are more variable (Appendix 1).

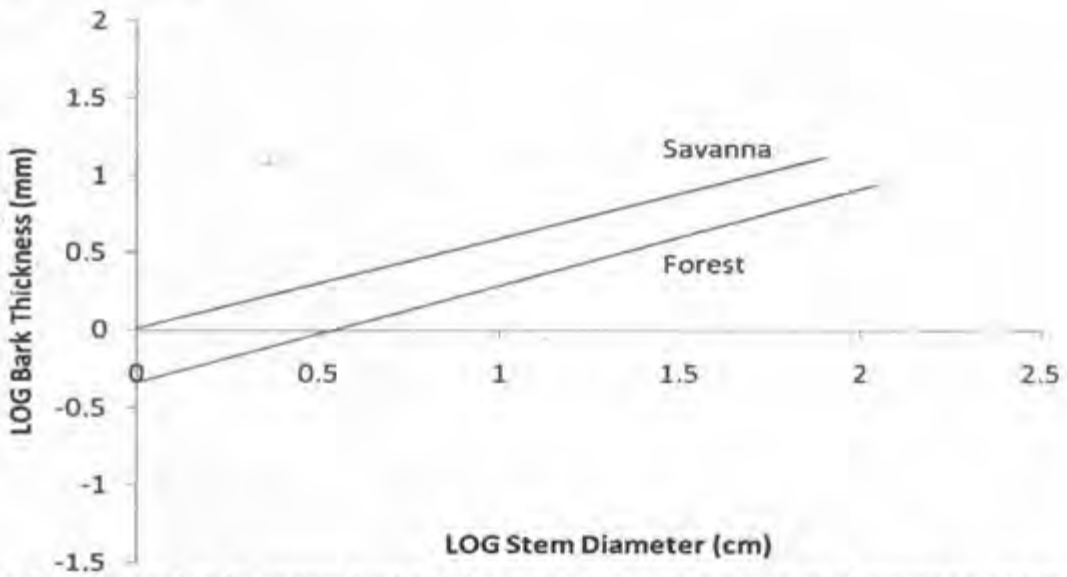

Figure 6. Relationship between bark thickness and stem diameter of all savanna and forest species. Both axes are log-transformed. Forest ($y = 0.6227x - 0.3365$, $R^2 = 0.39$, $p < 0.0001$, $n = 270$) Savanna ($y = 0.5798x + 0.0101$, $R^2 = 0.47$, $p < 0.0001$, $n = 270$).

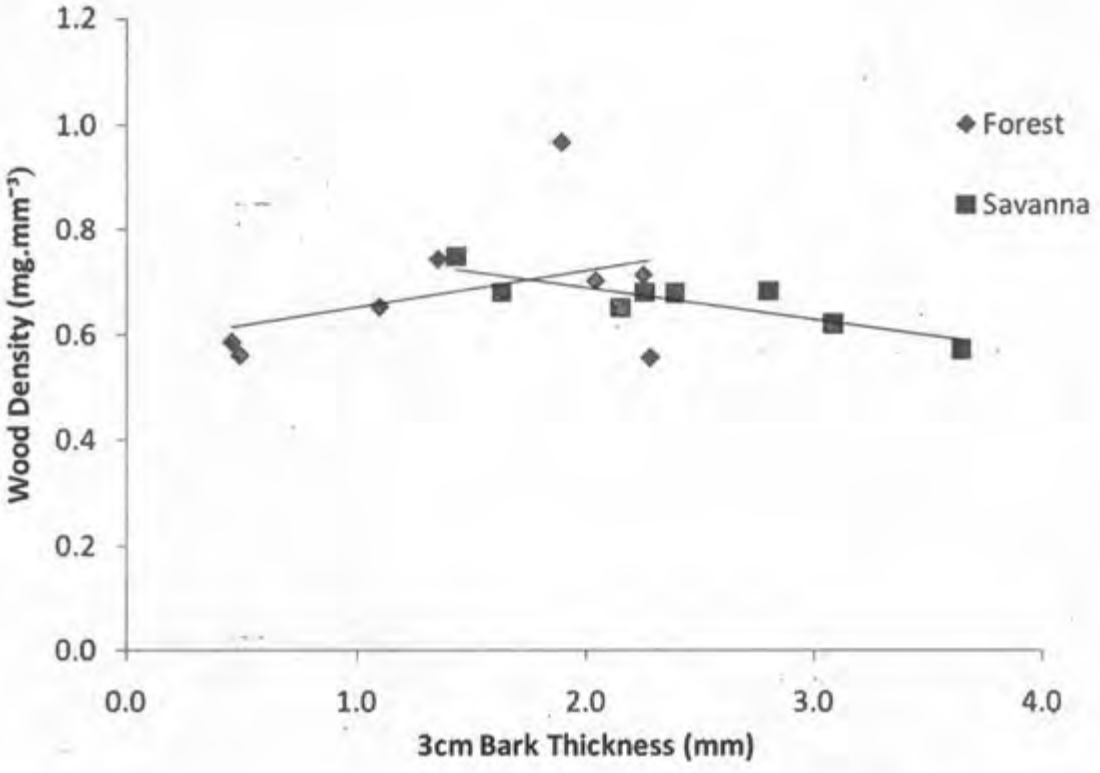

Figure 7. Relationship between wood density and bark thickness for all forest and savanna species excluding the Dombeya pair. Forest ($y = 0.0701x + 0.5823$, $R^2 = 0.15$, $p = 0.340$, $n = 8$) Savanna ($y = -0.0613x + 0.8131$, $R^2 = 0.75$, $p = 0.0157$, $n = 8$).

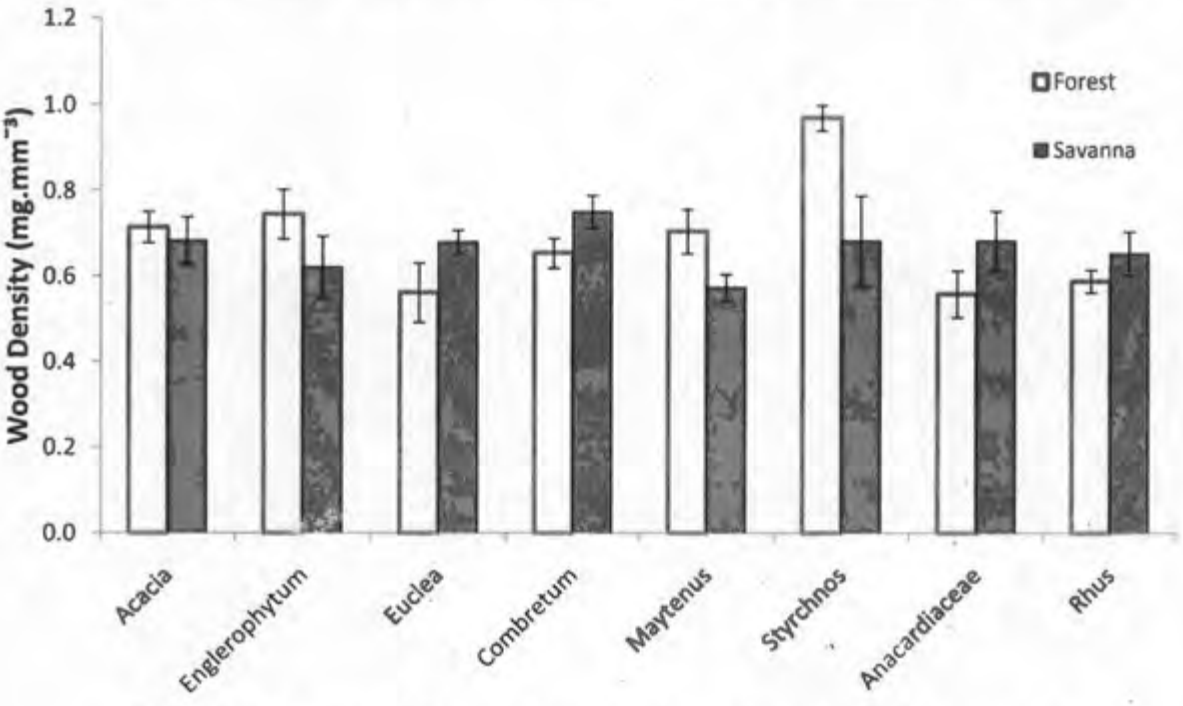

Figure 8. Mean Wood Density for each of the savanna and forest species. Error bars indicate standard deviation. See Table 1 for species names.

Table 2: Wood density for eight savanna and forest congeneric pairs with the results from a Kruskal-Wallis Multiple Comparison Test. Standard Deviations are indicated in parentheses.

	Mean Wood Density ($mg.mm^{-3}$)		Kruskal-Wallis Multiple Comparison			
	Forest	Savanna	H	N	P	df
Acacia	0.715 (0.037)	0.683 (0.056)	0.240	9	0.490	1
Englerophytum	0.745 (0.056)	0.621 (0.073)	0.398	10	0.047	1
Euclea	0.561 (0.070)	0.680 (0.028)	5.771	10	0.016	1
Combretum	0.654 (0.035)	0.749 (0.038)	6.818	10	0.009	1
Maytenus	0.704 (0.052)	0.572 (0.032)	6.818	10	0.009	1
Strychnos	0.967 (0.030)	0.681 (0.106)	5.333	8	0.021	1
Anacardiaceae	0.557 (0.054)	0.681 (0.690)	4.811	10	0.028	1
Rhus	0.587 (0.027)	0.651 (0.051)	4.811	10	0.028	1

Wood density was compared with 3cm stem diameter bark thickness (Figure 7). This stem diameter was chosen because the wood samples were generally taken from 3cm diameter branches. Savanna trees showed decreasing wood density with increasing bark thickness ($y = -0.0613x + 0.8131$, $R^2 = 0.75$, $p = 0.0157$, $n = 80$) although the relationship was not statistically significant. Forest trees showed a positive but weak relationship between bark thickness and wood density ($y = 0.0701x + 0.5823$, $R^2 = 0.15$, $p = 0.340$, $n = 80$). When compared within the pairs, the only pair not to show a significant difference in wood density between savanna and forest species was the Acacia pair ($H(1) = 0.240$, $p = 0.490$). The difference in wood density is not unidirectional; three pairs have forest species with greater wood density than the savanna counterpart (Table 2).

The stem profiles (Figure 9) generally show savanna species having thick branches with stem diameter increasing at a greater rate from the shoot tip than forest trees. The Euclea pair show an almost parallel relationship between *Euclea divinorum* ($y = 0.0159x - 0.0154$, $R^2 = 0.97$, $p < 0.0001$, $n = 30$) and *Euclea racemosa* ($y = 0.0163x + 0.0736$, $R^2 = 0.78$, $p < 0.0001$, $n = 30$). Three of the nine pairs show forest species having a larger diameter than savanna species 5cm from the shoot tip, two pairs show the savanna species having a larger diameter and four

species show no significant differences (Appendix 2).The stem profiles from Figure 9 were used in conjunction with bark thickness relationships in Figure 5 to produce Figure 10.

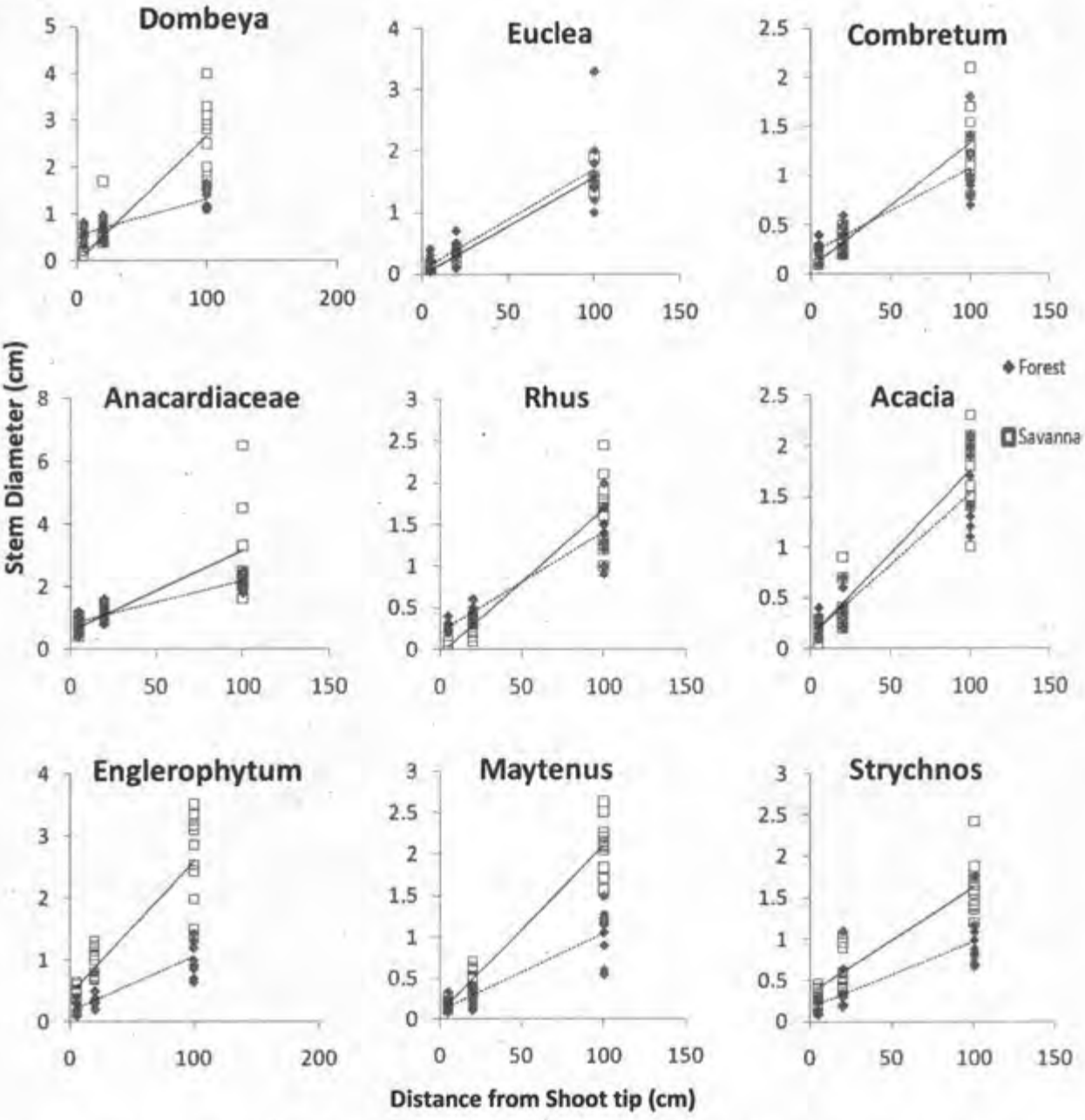

Figure 9. Relationship between the distance from the shoot tip and stem diameter of congeneric forest and savanna species pairs. See Table 1 for species names. Dotted line and solid line indicate Forest and Savanna regressions respectively. Statistics are listed in Appendix 3.

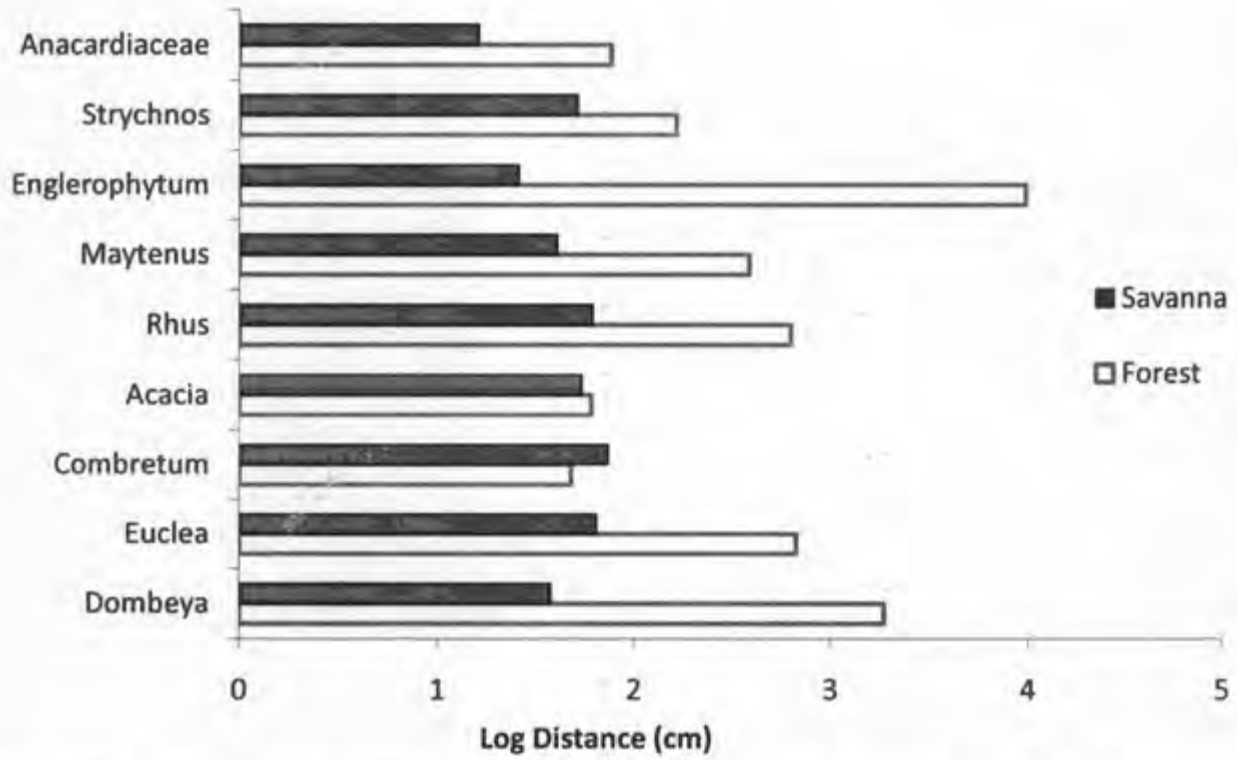

Figure 10: Distance from the shoot tip to a stem diameter which supports the average absolute bark thickness at 1cm diameter of the savanna species of each congeneric pair. Distance is log-transformed to show order of magnitude differences within the pairs.

If vulnerability of stems to fire injury depends on the bark thickness, then canopy die back will vary depending on its relationship between shoot length and bark thickness. Figure 10 shows the shoot length standardised relative to the savanna species with bark thickness measured at 1cm diameter. Forest species generally had much greater shoot lengths vulnerable to fire injury than savanna trees using this assumption (Figure 10). The only deviation from the trend was in the Combretum pair. The most extreme case was the Englerophytum pair. The distance on *Englerophytum natalense* was nearly three orders of magnitude larger than that of *Englerophytum magalismontanum* (Figure 10). The highest similarity was found in the Acacia pair where there was less than 0.04 order of magnitude difference (Figure 10).

Figure 11 and Figure 12 consistently show the lack of consistency in bud and resprout traits of savanna and forest species. The Combretum and Rhus pairs show significant differences in number of resprouts and the lengths of these resprouts for both treatments

(Appendix 2). The Acacia pair shows significant differences in the number of resprouts for the 1cm treatment and the number of buds and resprout length for the 3cm treatment. A one-tailed Mann-Whitney U-test revealed no significantly lower numbers of resprouts on the 3cm treated branch than on the 1cm treated branch for all species (Appendix 4).

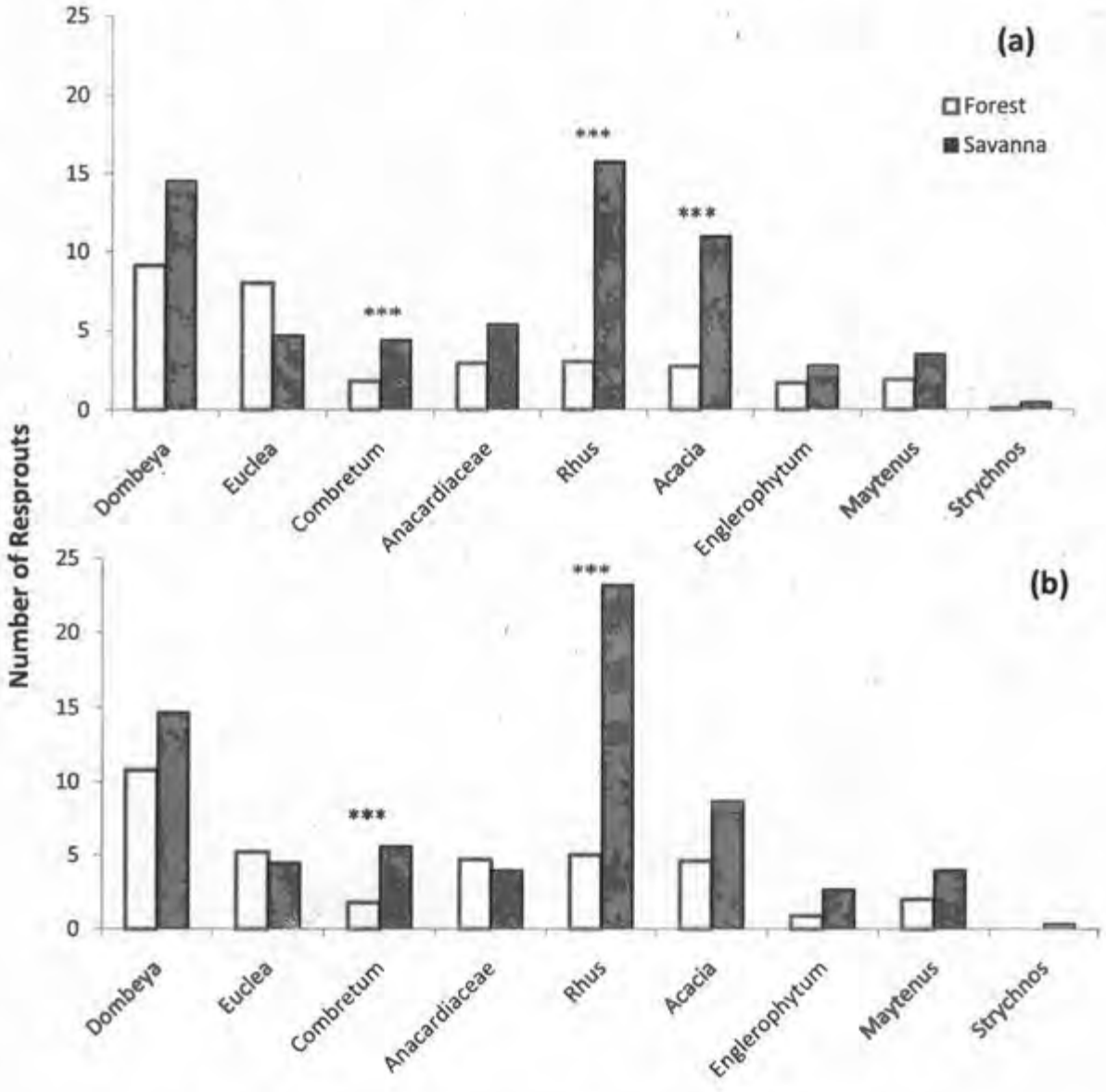

Figure 11. Average number of resprouts on each of the treated branches for both species of the congeneric pairs. (a) 1cm treatment (b) 3cm treatment. *** $P < 0.05$

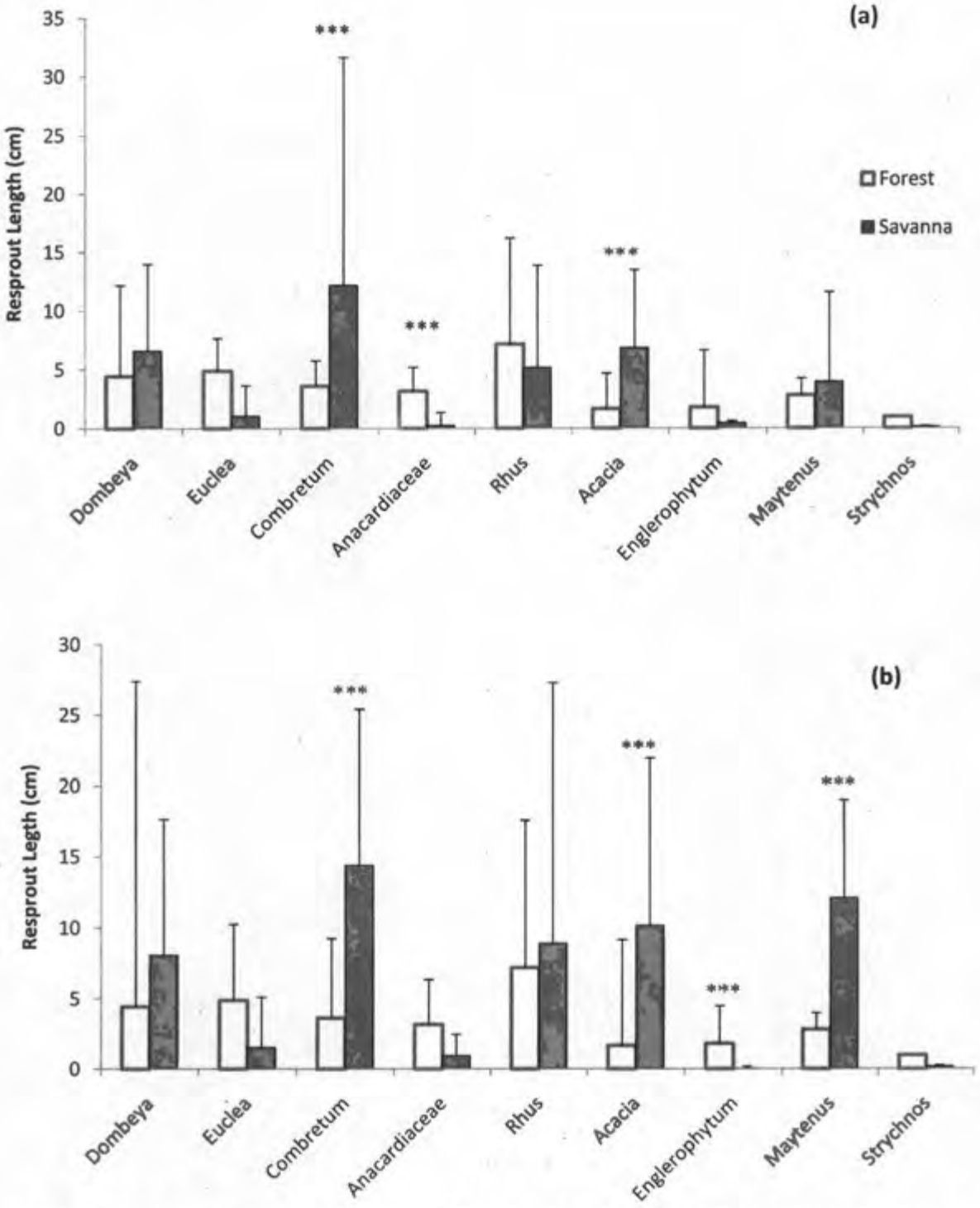

Figure 12. The median resprout length found on 1m of branch of each congeneric pair. Error bars indicate the mean maximum resprout length. (a) 1cm stem diameter treatment, (b) 3cm stem diameter treatment. *** $P < 0.05$

Data for forest and savanna species show a triangular relationship between tree height and the number of resprouts for both the 1cm and 3cm treatments (Figure 14). Taller trees have few resprouts whereas short trees are variable. Savanna trees are predominantly shorter with a higher number of resprouts, whereas the taller forest trees have less (Figure 13). The quantile regressions show savanna sprouting ability having a stronger negative relationship than forests (Figure 14). Forest trees maintain the ability to resprout in larger size classes where as the larger savanna trees, such as *Sclerocarya birrea,* show a decreased capacity to resprout.

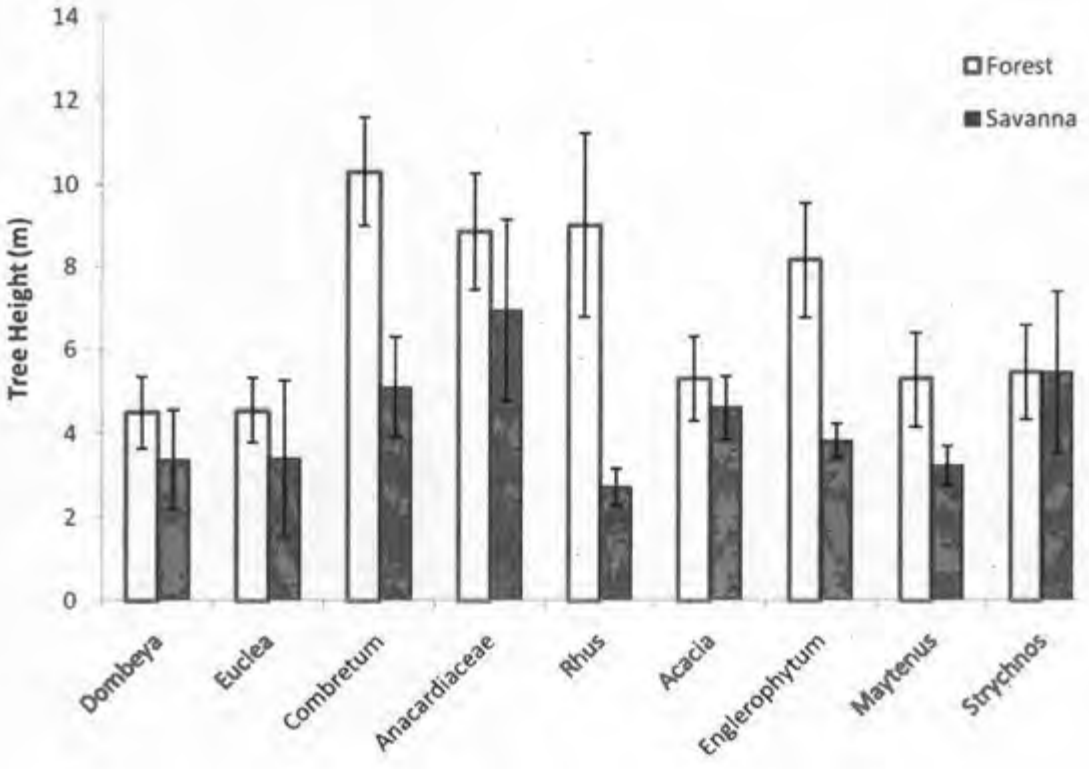

Figure 13. The mean tree height of the forest and savanna species of each congeneric pair. Error bars indicate Standard Deviation. See Table 1 for species names.

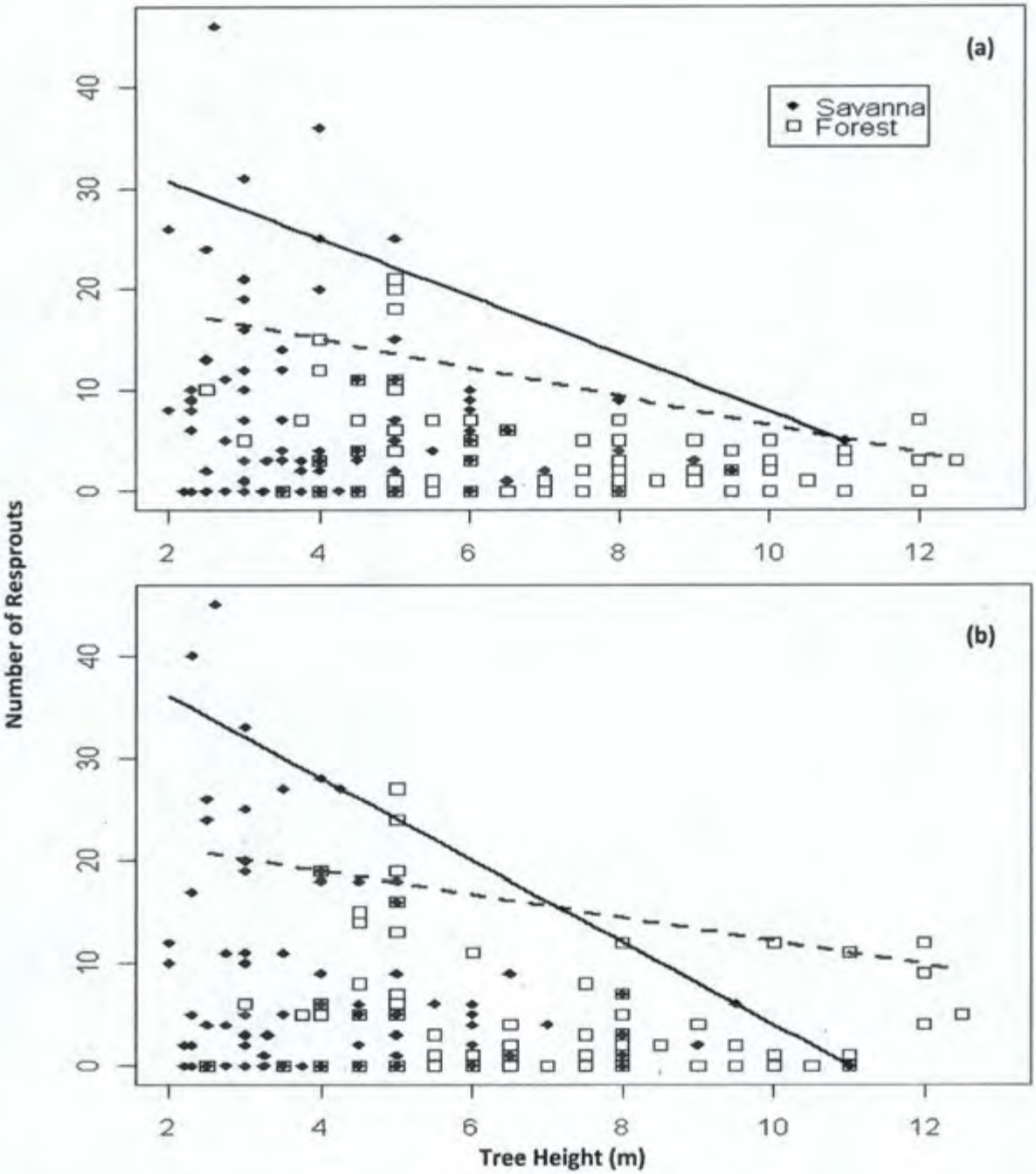

Figure 14. Relationship between tree height and the number of resprouts found on 1m of branch of each congeneric pair. (a) 1cm stem diameter treatment (b) 3cm stem diameter treatment. Dotted line and solid line indicate Forest and Savanna regressions respectively.

1cm Savanna: y = -2.857x + 36.429, Std. Error = 10.666, t value = 3.416, Pr (>|t|) = 0.001,
1cm Forest: y = -1.412x + 20.647, Std. Error = 2.463, t value = 8.384, Pr (>|t|) < 0.0001.
3cm Savanna: y = -4x + 44.0, Std. Error = 12.218, t value = 3.6014, Pr (>|t|) = 0.001,
3cm Forest: y = -1.143x + 23.571, Std. Error = 4.498, t value = 5.241, Pr (>|t|) < 0.0001.

Discussion

A fire in the Hluhluwe-iMfolozi Park on the 7th November 2004 (M. Waldram, *pers comm.*), caused the death of large trees within the Phindisweni Forest (*pers observation*). Char height observations within the forest indicate that the flames were approximately 1m high at most (W. Bond, *pers comm.*). Despite the low intensity of this surface fire, large trees with thick bark, such as *Protorhus longifolia* and *Ekebergia capensis*, died or resprouted basally (J. Midgley, unpublished data). The canopy scorch from this low intensity fire was adequate disturbance to cause the death of these adult forest trees, whereas in savannas, adult trees can recover their canopies after scorching through epicormic resprouting (Browne, *Unpublished*; Bond and Midgley, 2001). This study explored two of the possible mechanisms for this difference in crown resprouting following canopy scorch: (1) differences in bud banks and their insulation, (2) differences in the vulnerability to disruption of the hydraulic system by heat scorch.

Savanna trees have thicker bark than forest trees

In most congeneric pairs, the savanna species display a significantly greater bark thickness at a 1cm diameter. Essentially, savanna species invest in thicker bark for canopy shoots than forest species to increase resistance to fire. This can be seen in the stem architecture measurements where the profiles of the savanna species show greater rates of increase in stem diameter than their congeneric counterparts. Investment in defence is known to be a trade-off against increase in size (Jackson *et al*, 1999; Hoffman *et al*, 2003; Archibald and Bond, 2003), which could explain the delay in investment by forest trees. The ability to outcompete neighbouring plants for light is a vital trait for forest species (Jackson *et al*, 1999). Compromising on the rate of growth for increased defence is an unnecessary precaution for species subject to an infrequent fire regime (Jackson *et al*, 1999, Archibald and Bond, 2003). Savanna trees on the other hand, do not compete for light (Archibald and Bond, 2003); instead, they experience regular burns (Hoffman *et al*, 2009) which most likely selects for the investment in structural "defence" in the juvenile stage and insulation of the buds in the adult stage.

Viable bud banks

The greater insulation of tissues by savanna species is particularly evident in Figure 10. If vulnerability, and hence canopy die back, depends on absolute bark thickness, savanna species with the exception of *Combretum* molle, will lose less of their canopy compared to forest species from a uniform fire intensity. For both *Englerophytum natalense* and *Dombeya burgessii*, not one individual reached a diameter with a 'safe' absolute bark thickness. If the mechanism for crown resprouting following canopy scorch is the presence of a viable bud bank; we would expect to see differences in the number of resprouts between the two treatments for forest trees. Effectively, forest trees would not have a viable bud bank on thicker branches from which to resprout and the greater canopy die back (proposed in Figure 10) would eliminate the possibility of recovery. Savanna trees, supposedly, would show a similar capacity for resprouting at large and small stem diameters. With the exception of *Englerophytum magalismontanum*, the results from the Mann-Whitney U-test show no statistically significant decrease in bud banks and sprouting ability from the 1cm to the 3cm stem diameter treatment (Appendix 4). *Englerophytum magalismontanum* shows a decrease in the ability to resprout at larger diameters; this could be, in part, due to the timing of the treatment for this particular species which was later than the other species.

Resprouting vigour

The ability to resprout does not differ consistently between forest and savanna species, contrary to predictions. *Combretum molle, Rhus pentheri* and *Acacia karroo* show significantly greater numbers of resprouts found on a branch to their respective congeneric forest counterparts (Figure 11). No congeneric pair shows a significantly higher number of resprouts on the forest species (Appendix 2). There are different strategies in the allocation of resources to resprouting; *Rhus pentheri*, which shows a significantly greater number of resprouts than *Rhus chirindensis*, shows no difference in median resprout length. The Maytenus pair shows the opposite of this relationship with a difference in median lengths but not in the number of resprouts (Figure 11 and Figure 12). I hypothesized that savanna species would demonstrate a superior ability, to the congeneric forest species, to recover their canopies by resprouting

however, this was not the case. Gignoux *et al* (1997) defined two fire resistance strategies for *Crossopteryx* and *Piliostigma*. One strategy is that of resisting structural damage by fire through the defence of above-ground structures. The other is the ability to recover aboveground structures by post-burn resprouting. The two strategies proposed by Gignoux *et al* (1997) neglect the importance of the height of individual trees. The resistance strategy refers only to defence and not avoidance. In savanna species; tree height was a limiting factor for the number of resprouts of larger individuals whereas for smaller individuals; resprouting was controlled by a multitude of factors (Figure 14). For forest trees, the same negative relationship was observed although not as pronounced (Figure 14).The importance of resprouting as a recovery strategy decreases with larger individuals (Midgley, 1996).

Vulnerability to hydraulic failure

Balfour and Midgley (2006) showed that the death of canopy buds is insufficient to cause tree death of *Acacia karroo* and propose heat-induced damage to the xylem as a possible mechanism for tree death as suggested by Ducrey *et al* (1996). The post-fire recovery of trees would therefore be influenced by the vulnerability of the hydraulic system to xylem malfunction (Balfour and Midgley, 2006). Hacke *et al* (2001) presented a positive relationship between the reinforcement of conduit walls and the prevention of xylem malfunction. Wood density is a reliable predictor of this reinforcement (Hacke *et al*, 2001), hence its use in this study as a measure of vulnerability to hydraulic failure.

As is the case with resprouting ability; wood density does not differ consistently between forest and savanna species (Table 2). With the exception of *Acacia*, the congeneric pairs show a significant difference is wood density between savanna and forest species; however the trend is not consistent (Table 2). The *Euclea*, *Combretum*, *Anacardiaceae* and *Rhus* congeneric pairs show the predicted pattern; savanna trees have a higher wood density to prevent xylem malfunction during heating (Table 2). This is not the case for the *Englerophytum*, *Strychnos* and *Maytenus* pairs. Investment in wood density has been shown by Enquist *et al* (1999) to have a negative effect of growth rate. *Strychnos henningsii*, *Englerophytum natalense* and *Maytenus mossambicensis* are shade tolerant forest species (Orwa *et al*, 2009); it is

possible that the higher wood density is the result of a slower growth rate and not a precaution against heat-induced hydraulic failure (Enquist *et al*, 1999). The greater bark thickness of savanna species may be to insulate the xylem vessels and not the buds (Balfour and Midgley, 2006), however this study provides no conclusive evidence of differences in the relationship between bark thickness and wood density of congeneric savanna and forest species (Figure 7).

Conclusions

The proposal of two mechanisms for the differences in forest and savanna crown recovery after canopy scorch is most likely an oversimplification of a suite of strategies. The varied response of the congeneric pairs is a testament to this. Contrary to predictions, there was no difference in congeneric forest and savanna species ability to resprout at thicker stem diameters. Therefore, provided a forest tree reaches a 'safe' absolute bark thickness, the predicted canopy die back will not influence the presence of a bud banks or the ability to resprout. The accuracy of this result could be improved by modifying the treatments to remove stems at a standardized bark thickness rather than set stem diameters. There are a range of responses in terms of resprouting capability and vigour with neither savanna nor forest species showing a clear dominance over the other. The greater bark thickness of savanna species may insulate xylem vessels instead of the buds and/or the cambium. The wood density measurements were inconclusive, the influence of life history traits, such as shade tolerance in some forest species, may affect the integrity of wood density as a measurement of vulnerability to heat-induced hydraulic failure.

Some savanna species, such as *Combretum molle* and *Rhus pentheri,* show significantly greater bark thickness, resprouting ability and wood density than their respective congeneric forest counterparts. However, these simulated crown scorch results require empirical evidence of congeneric forest-savanna species recovery or mortality following crown scorch to validate the predicted responses.

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Appendix 1

Table 3. Least Squares Regression statistics for the relationship between bark thickness and stem diameter for savanna and forest pairs.

	Regression Equation		R^2		n		P		df	
	Forest Species	Savanna Species	Forest Species	Savanna Species	Forest Species	Savanna Species	Forest Species	Savanna Species	Forest Species	Savanna Species
Dombeya	y = 0.7988x - 0.8685	y = 0.6969x - 0.0329	0.44	0.31	30	30	0.0001	0.0017	1.28	1.28
Euclea	y = 0.6208x - 0.6771	y = 0.7574x - 0.0367	0.42	0.87	30	30	0.0001	< 0.0001	1.28	1.28
Combretum	y = 0.2462x - 0.1787	y = 0.7394x - 0.2527	0.40	0.71	30	30	0.0002	< 0.0001	1.28	1.28
Anacardiaceae	y = 0.7996x - 0.1207	y = 0.7159x - 0.2435	0.90	0.52	30	30	< 0.0001	< 0.0001	1.28	1.28
Rhus	y = 0.9584x - 0.7899	y = 0.5781x + 0.0227	0.74	0.51	30	30	< 0.0001	< 0.0001	1.28	1.28
Acacia	y = 0.851x - 0.11	y = 1.1817x - 0.1721	0.78	0.80	30	30	< 0.0001	< 0.0001	1.28	1.28
Englerophytum	y = 0.1197x - 0.029	y = 0.387x + 0.234	0.13	0.83	30	30	0.0524	< 0.0001	1.28	1.28
Strychnos	y = 0.7123x - 0.1286	y = 0.3292x + 0.0706	0.85	0.68	30	30	< 0.0001	< 0.0001	1.28	1.28
Maytenus	y = 0.5923x - 0.1257	y = 0.5126x + 0.2249	0.55	0.70	30	30	< 0.0001	< 0.0001	1.28	1.28
All Trees	y = 0.6227x - 0.3365	y = 0.5798x + 0.0101	0.39	0.47	270	270	< 0.0001	< 0.0001	1.268	1.268

Appendix 2.1

Table 4a. Mann-Whitney U-test statistics of multiple variables for savanna and forest pairs.

	Dombeya					Euclea					Combretum				
	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P
1cm Bark Thickness (mm)	66.5	143.5	11.5	-2.92126	0.0035	60.0	150.0	5.0	-3.41829	0.0006	102.5	107.5	47.5	-0.15363	0.8779
3cm Bark Thickness (mm)	55.0	155.0	0.0	-3.74749	0.0002	55.0	155.0	0.0	-3.76313	0.0002	80.0	130.0	25.0	-1.87112	0.0613
1m Trunk Relative Bark Thickness	55.0	155.0	0.0	-3.74185	0.0002	55.0	155.0	0.0	-3.74326	0.0002	57.0	153.0	2.0	-3.59066	0.0003
5cm Stem diameter	155.0	55.0	0.0	3.86903	0.0001	102.0	108.0	47.0	-0.19912	0.8422	141.0	69.0	14.0	2.94012	0.0033
20cm Stem diameter	138.5	71.5	16.5	2.58143	0.0098	140.0	70.0	15.0	2.66885	0.0076	119.5	90.5	35.5	1.08773	0.2767
100cm Stem diameter	55.0	155.0	0.0	-3.74890	0.0002	103.0	107.0	48.0	-0.11456	0.9088	84.0	126.0	29.0	-1.55551	0.1198
1cm Number of Resprouts	72.0	99.0	27.0	-1.15030	0.2500	105.0	85.0	30.0	1.19444	0.2323	71.5	138.5	16.5	-2.52318	0.0116
3cm Number of Resprouts	99.0	111.0	44.0	-0.41654	0.6770	109.0	101.0	46.0	0.27139	0.7861	71.0	139.0	16.0	-2.57033	0.0102
1cm Number of Functioning Buds	81.5	89.5	36.5	-0.31083	0.7559	108.5	81.5	26.5	1.48475	0.1376	77.5	132.5	22.5	-2.07806	0.0377
3cm Number of Functioning Buds	107.5	102.5	47.5	0.15251	0.8788	103.0	107.0	48.0	-0.11640	0.9073	72.0	138.0	17.0	-2.49457	0.0126
1cm Total Resprout Length	90.0	120.0	35.0	-1.09775	0.2723	119.0	91.0	36.0	1.02826	0.3038	69.5	140.5	14.5	-2.64774	0.0081
3cm Total Resprout Length	109.0	101.0	46.0	0.26458	0.7913	112.0	98.0	43.0	0.50204	0.6156	76.0	134.0	21.0	-2.17161	0.0299

Appendix 2.2

Table 4b. Mann-Whitney U-test statistics of multiple variables for savanna and forest pairs.

	Anacardiaceae					Rhus					Acacia				
	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P
1cm Bark Thickness (mm)	100.0	110.0	45.0	-0.35060	0.7259	60.5	149.5	5.5	-3.40643	0.0007	96.5	113.5	41.5	-0.64367	0.5198
3cm Bark Thickness (mm)	125.0	85.0	30.0	1.47907	0.1391	55.0	155.0	0.0	-3.79648	0.0001	90.0	120.0	35.0	-1.13290	0.2573
1m Trunk Relative Bark Thickness	127.0	83.0	28.0	1.62525	0.1041	127.0	83.0	28.0	1.62525	0.1041	88.0	122.0	33.0	-1.24728	0.2123
5cm Stem diameter	111.5	98.5	43.5	0.45753	0.6473	155.0	55.0	0.0	3.82771	0.0001	124.0	86.0	31.0	1.46436	0.1431
20cm Stem diameter	124.0	86.0	31.0	1.41451	0.1572	149.0	61.0	6.0	3.33115	0.0009	88.5	121.5	33.5	-1.25769	0.2085
100cm Stem diameter	84.5	125.5	29.5	-1.52627	0.1269	84.0	126.0	29.0	-1.55434	0.1201	88.0	122.0	33.0	-1.25247	0.2104
1cm Number of Resprouts	82.0	128.0	27.0	-1.72301	0.0849	69.5	140.5	14.5	-2.65777	0.0079	79.5	130.5	24.5	-2.06957	0.0385
3cm Number of Resprouts	104.0	106.0	49.0	-0.03844	0.9693	57.5	152.5	2.5	-3.56091	0.0004	81.5	128.5	26.5	-1.79845	0.0721
1cm Number of Functioning Buds	80.5	129.5	25.5	-1.83293	0.0668	70.5	139.5	15.5	-2.58773	0.0097	82.0	128.0	27.0	-1.86178	0.0626
3cm Number of Functioning Buds	103.5	106.5	48.5	-0.07724	0.9384	59.0	151.0	4.0	-3.44987	0.0006	79.0	131.0	24.0	-1.99314	0.0462
1cm Total Resprout Length	123.5	86.5	31.5	1.36118	0.1735	83.5	126.5	28.5	-1.59345	0.1111	81.0	129.0	26.0	-1.94452	0.0518
3cm Total Resprout Length	116.0	94.0	39.0	0.80438	0.4212	66.0	144.0	11.0	-2.91033	0.0036	78.5	131.5	23.5	-2.03058	0.0423

Appendix 2.3

Table 4c. Mann-Whitney U-test statistics of multiple variables for savanna and forest pairs.

	Englerophytum					Strychnos					Maytenus				
	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P	Forest Mean Rank	Savanna Mean Rank	U	2-tailed Z score	P
1cm Bark Thickness (mm)	60.0	150.0	5.0	-3.38430	0.0007	74.5	135.5	19.5	-2.30447	0.0212	69.0	141.0	14.0	-2.69166	0.0071
3cm Bark Thickness (mm)	55.0	155.0	0.0	-3.76027	0.0002	86.0	124.0	31.0	-1.40269	0.1607	55.5	154.5	0.5	-3.71244	0.0002
1m Trunk Relative Bark Thickness	63.0	147.0	8.0	-3.13829	0.0017	153.0	57.0	2.0	3.59066	0.0003	57.0	153.0	2.0	-3.59066	0.0003
5cm Stem diameter	57.0	153.0	2.0	-3.60015	0.0003	62.5	147.5	7.5	-3.18089	0.0015	107.5	102.5	47.5	0.15210	0.8791
20cm Stem diameter	59.0	151.0	4.0	-3.44596	0.0006	71.0	139.0	16.0	-2.53427	0.0113	70.5	139.5	15.5	-2.58183	0.0098
100cm Stem diameter	56.0	154.0	1.0	-3.67178	0.0002	63.0	147.0	8.0	-3.13711	0.0017	55.0	155.0	0.0	-3.74326	0.0002
1cm Number of Resprouts	91.5	118.5	36.5	-1.02396	0.3059	99.0	111.0	44.0	-0.66879	0.5036	91.0	119.0	36.0	-1.05860	0.2898
3cm Number of Resprouts	122.5	87.5	32.5	1.58890	0.1121	95.0	115.0	40.0	-1.38032	0.1675	87.0	123.0	32.0	-1.34847	0.1775
1cm Number of Functioning Buds	91.5	118.5	36.5	-1.02396	0.3059	99.0	111.0	44.0	-0.66879	0.5036	90.0	120.0	35.0	-1.13655	0.2557
3cm Number of Functioning Buds	122.5	87.5	32.5	1.58890	0.1121	95.0	115.0	40.0	-1.38032	0.1675	87.5	122.5	32.5	-1.31045	0.1900
1cm Total Resprout Length	106.0	104.0	49.0	0.03907	0.9688	101.0	109.0	46.0	-0.42559	0.6704	93.5	116.5	38.5	-0.85909	0.3903
3cm Total Resprout Length	125.5	84.5	29.5	1.86394	0.0623	95.0	115.0	40.0	-1.37840	0.1681	79.0	131.0	24.0	-1.95349	0.0508

Appendix 3

Table 5. Least Squares Regression statistics for the relationship between the distance from the shoot tip and stem diameter for savanna and forest pairs.

	Regression Equation		R^2		N		P		df	
	Forest Species	Savanna Species	Forest Species	Savanna Species	Forest Species	Savanna Species	Forest Species	Savanna Species	Forest Species	Savanna Species
Dombeya	y=0.0077x + 0.5583	y = 0.0266x + 0.001	0.76	0.86	30	30	< 0.0001	< 0.0001	1.28	1.28
Euclea	y = 0.0163x + 0.0736	y = 0.0159x - 0.0154	0.78	0.97	30	30	< 0.0001	< 0.0001	1.28	1.28
Combretum	y = 0.0086x + 0.215	y = 0.0127x + 0.0686	0.75	0.86	30	30	< 0.0001	< 0.0001	1.28	1.28
Anacardiaceae	y = 0.0133x + 0.841	y = 0.0257x + 0.5879	0.82	0.61	30	30	< 0.0001	< 0.0001	1.28	1.28
Rhus	y = 0.012x + 0.2057	y = 0.0173x - 0.0562	0.87	0.90	30	30	< 0.0001	< 0.0001	1.28	1.28
Acacia	y = 0.014x + 0.1323	y = 0.0164x + 0.1182	0.87	0.88	30	30	< 0.0001	< 0.0001	1.28	1.28
Englerophytum	y = 0.0087x + 0.1769	y = 0.0215x + 0.448	0.80	0.81	30	30	< 0.0001	< 0.0001	1.28	1.28
Strychnos	y = 0.008x + 0.1623	y = 0.0129x + 0.3401	0.65	0.83	30	30	< 0.0001	< 0.0001	1.28	1.28
Maytenus	y = 0.0093x + 0.1119	y = 0.0203x + 0.0738	0.83	0.95	30	30	< 0.0001	< 0.0001	1.28	1.28

Appendix 4.1

Table 6a. Mann-Whitney U-test statistics of differences in resprouting capability between the 1cm and 3cm treatments for savanna and forest species.

	Dombeya burgessii					Dombeya rotundifolia				
	1cm Rank Sum	3cm Rank Sum	U	2-tailed Z score	P	1cm Rank Sum	3cm Rank Sum	U	2-tailed Z score	P
Number of Resprouts	85.0	105.0	40.0	-0.369	0.712	92.0	98.0	43.0	0.123	0.902
Number of Functioning Buds	96.5	93.5	38.5	0.493	0.622	98.0	92.0	37.0	0.617	0.537
Total Resprout Length	58.5	131.5	13.5	-2.532	0.011	92.0	98.0	43.0	0.122	0.903
Median Bud Length	59.0	131.0	14.0	-2.493	0.013	87.5	102.5	42.5	-0.163	0.870
Maximum Bud Length	67.0	123.0	22.0	-1.840	0.066	88.5	101.5	43.5	-0.082	0.935

	Euclea racemosa					Euclea divinorum				
	1cm Rank Sum	3cm Rank Sum	U	2-tailed Z score	P	1cm Rank Sum	3cm Rank Sum	U	2-tailed Z score	P
Number of Resprouts	102.0	88.0	33.0	0.950	0.342	108.5	101.5	46.5	0.230	0.818
Number of Functioning Buds	109.0	81.0	26.0	1.527	0.127	106.5	103.5	48.5	0.077	0.939
Total Resprout Length	99.0	91.0	36.0	0.700	0.484	103.5	106.5	48.5	-0.077	0.939
Median Bud Length	100.0	90.0	35.0	0.783	0.433	96.5	113.5	41.5	-0.614	0.539
Maximum Bud Length	93.0	97.0	42.0	0.206	0.837	100.0	110.0	45.0	-0.345	0.730

	Combretum kraussii					Combretum molle				
	1cm Rank Sum	3cm Rank Sum	U	2-tailed Z score	P	1cm Rank Sum	3cm Rank Sum	U	2-tailed Z score	P
Number of Resprouts	118.5	91.5	36.5	1.012	0.311	97.5	112.5	42.5	-0.534	0.594
Number of Functioning Buds	120.5	89.5	34.5	1.170	0.242	109.5	100.5	45.5	0.308	0.758
Total Resprout Length	114.0	96.0	41.0	0.657	0.511	98.0	112.0	43.0	-0.491	0.623
Median Bud Length	113.0	97.0	42.0	0.580	0.562	91.5	118.5	36.5	-0.986	0.324
Maximum Bud Length	112.0	98.0	43.0	0.502	0.616	111.5	98.5	43.5	0.454	0.650